MORPHOLOGICAL STUDIES IN CORDYLINE (AGAVACEAE) II. VEGETATIVE MORPHOLOGY OF CORDYLINE TERMINALIS

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In an introductory paper in this series we described in a general way the growth habit of many species of *Cordyline* and the way it is related to a distinctive seedling morphology (Tomlinson & Fisher, 1971). We now restrict our inquiry to *C. terminalis*, the most widely cultivated species, describing its vegetative morphology in detail. This is the first comprehensive study of branching pattern in any member of the Agavaceae (*sensu* Hutchinson, 1959), and serves as a basis for future experimental work on the controlling factors of apical dominance, rhizome initiation, and secondary growth in this species. The continuing work will be reported in future articles. *Cordyline terminalis* grows rapidly and is easily propagated clonally so that it is an ideal experimental subject. It is therefore more suitable for experimental analysis than *Dracaena fragrans*, which was used initially as a subject for a reappraisal of the structure and growth of monocotyledons with secondary thickening (Tomlinson & Zimmermann, 1969; Zimmermann & Tomlinson, 1969; 1970).

Cordyline terminalis is probably native to the western Pacific and was at one time widely used as a food plant throughout Oceania (Barrau, 1961). The starchy underground rhizomes, erroneously called "root tubers," were cooked before being eaten. The leaves were used to wrap food, as a source of fiber, and even as clothing (largely ornamental). These uses have been supplanted by other food crops, but *C. terminalis* is still a widely cultivated ornamental. It forms, for example, the chief constituent of the living fences around the "gardens" of villagers in the highlands of New Guinea. There are numerous varieties referred to in horticultural literature (e.g., Graf, 1963). These differ chiefly in the color, shape, and size of the foliage leaves.

The usefulness of the shoot system of this species for experimental morphology was appreciated by Sachs (1882) and Goebel (1905) but their studies were preliminary and inconclusive. The underground rhizomes were described briefly by Troll (1937; p. 722).

MATERIAL AND METHODS

Most observations were made on large, field-grown plants up to 20 feet tall growing at Shaw's Nursery, 57th Ave., South Miami, Florida. These specimens included several varieties of unknown origin. Seeds were collected from mature fruits and sown in pots in a greenhouse to provide plants in early stages of development.
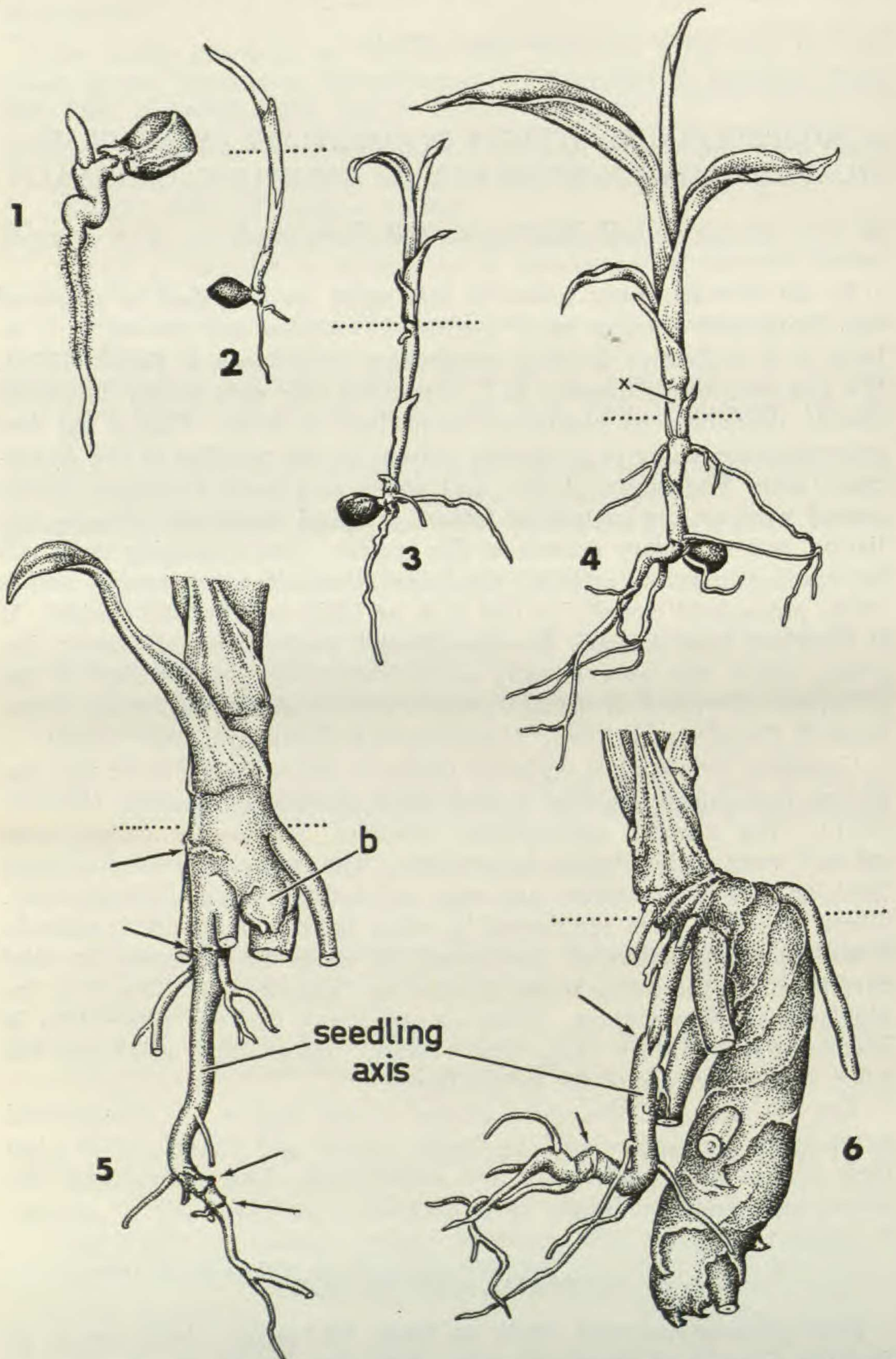
FIGURES 1–6. **Cordyline terminalis**, seedling. 1, early stage, plumule erect, cotyledon retained within seed, $\times$ 2 2/3; 2, later stage with scale leaves on plumule, $\times$ 1 1/3; 3, older seedlings with elongated internodes and adventitious roots, $\times$ 1 1/3; 4, still older seedling with distal foliage leaves $\times$ 1 1/3, X–inter-

For general anatomical observation, free-hand sections of fresh or FAA-fixed material were stained with aqueous solutions of either toluidine blue or basic fuchsin.

SEEDLING DEVELOPMENT

Germination in *Cordyline terminalis* is hypogeous (FIGURE 1), the greater part of the cotyledon remaining within the seed, and both cotyledon and seed remaining below soil level. This contrasts with the epigeous germination of *C. australis* and *C. banksii* which we have described and illustrated elsewhere (Tomlinson & Fisher, 1971; *Figs. 1, 2*). In these species only the tip of the cotyledon remains within the seed, the whole organ elongating and becoming erect; usually bringing the seed with it. Despite these early differences, late stages of seedling growth seem very similar in all species of *Cordyline*. The early differences are much more pronounced than those which Arnott (1962; p. 47) described in *Yucca* when he distinguished "hypogeous" from "epigeous" species. In both his types, the cotyledon does rise above the soil surface, although its tip is still within the seed coat, which may or may not remain buried. Later stages of *C. terminalis* are illustrated in FIGURES 2–6. The first plumular leaves are scale-like and there is a gradual transition to progressively larger foliage leaves. This should be contrasted with *C. australis*, where plumular leaves, though reduced, are green and never scale-like (cf. Tomlinson & Fisher, 1971; *Figs. 1–4*). The lowest, often underground, internodes are sometimes elongated (FIGURES 2–4), as in *C. australis*. Adventitious roots are developed on all parts of the seedling axis, but predominantly at the nodes. Successive internodes are progressively wider (FIGURE 5) in the manner normal for establishment growth in monocotyledons (Tomlinson & Zimmermann, 1966).

A major departure from normal monocotyledonous seedling development is then seen with the production of a descending (positively geotropic) rhizome from a bud in the axil of one of the lowest leaves (FIGURE 5, b). This repeats the peculiar pattern of seedling growth we described for other *Cordyline* species, in which the original seedling axis, displaced by this lateral rhizome, persists only as a pseudolateral appendage on older seedlings (FIGURE 6).

POST-SEEDLING DEVELOPMENT

The sapling subsequently develops as an apparently single axis which consists of the ascending, foliage-bearing aërial shoot continuous below

node in which secondary vascular cambium first develops; 5, base of mature seedling, rhizome bud at b; 6, later stage with seedling rhizome well developed × 2 2/3, the original seedling axis as an apparent appendage. Arrows indicate nodes on original seedling axis. Larger roots cut off in FIGURES 5 and 6. A diagram representing FIGURE 6 is given in FIGURE 7 A.
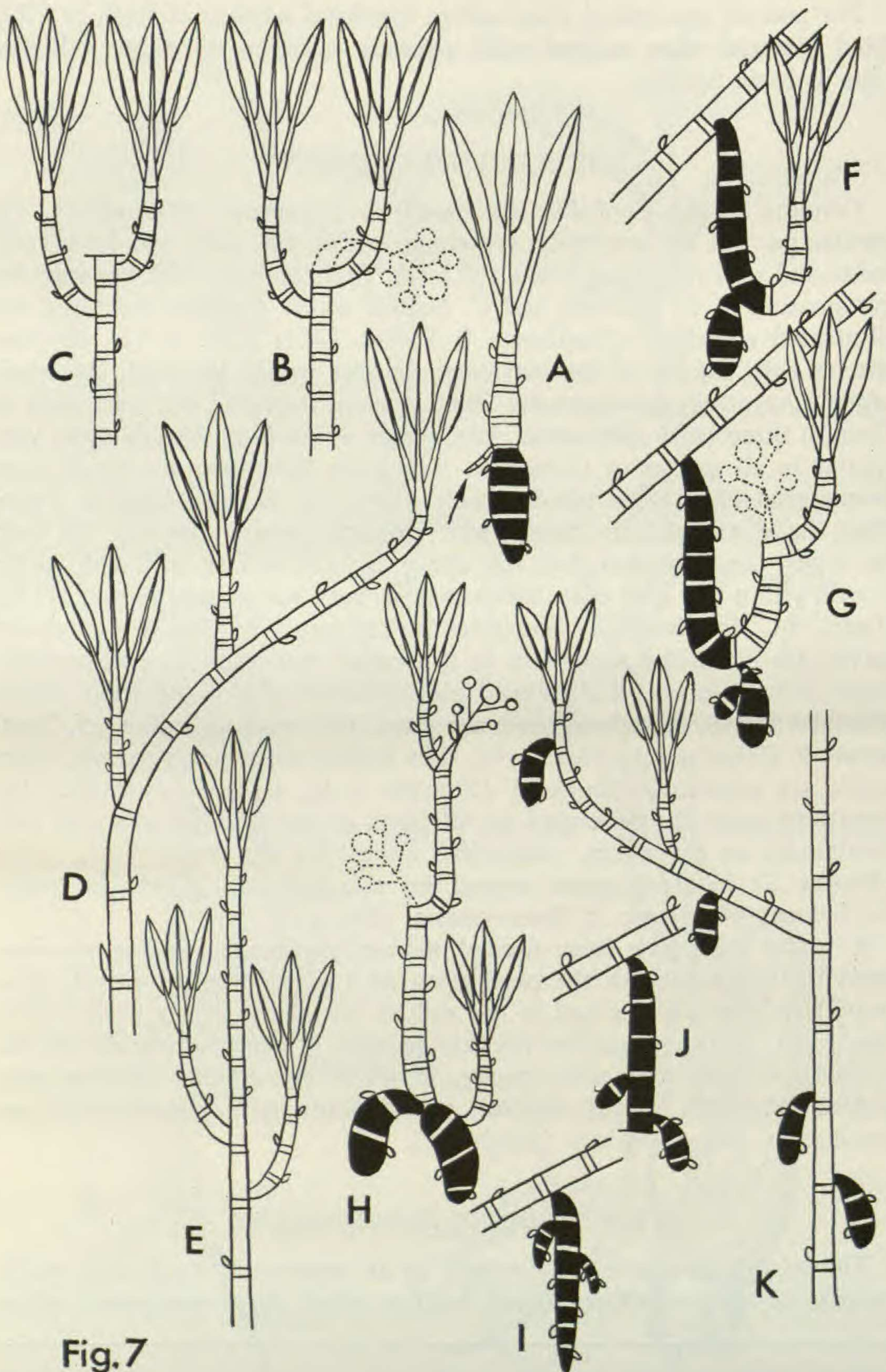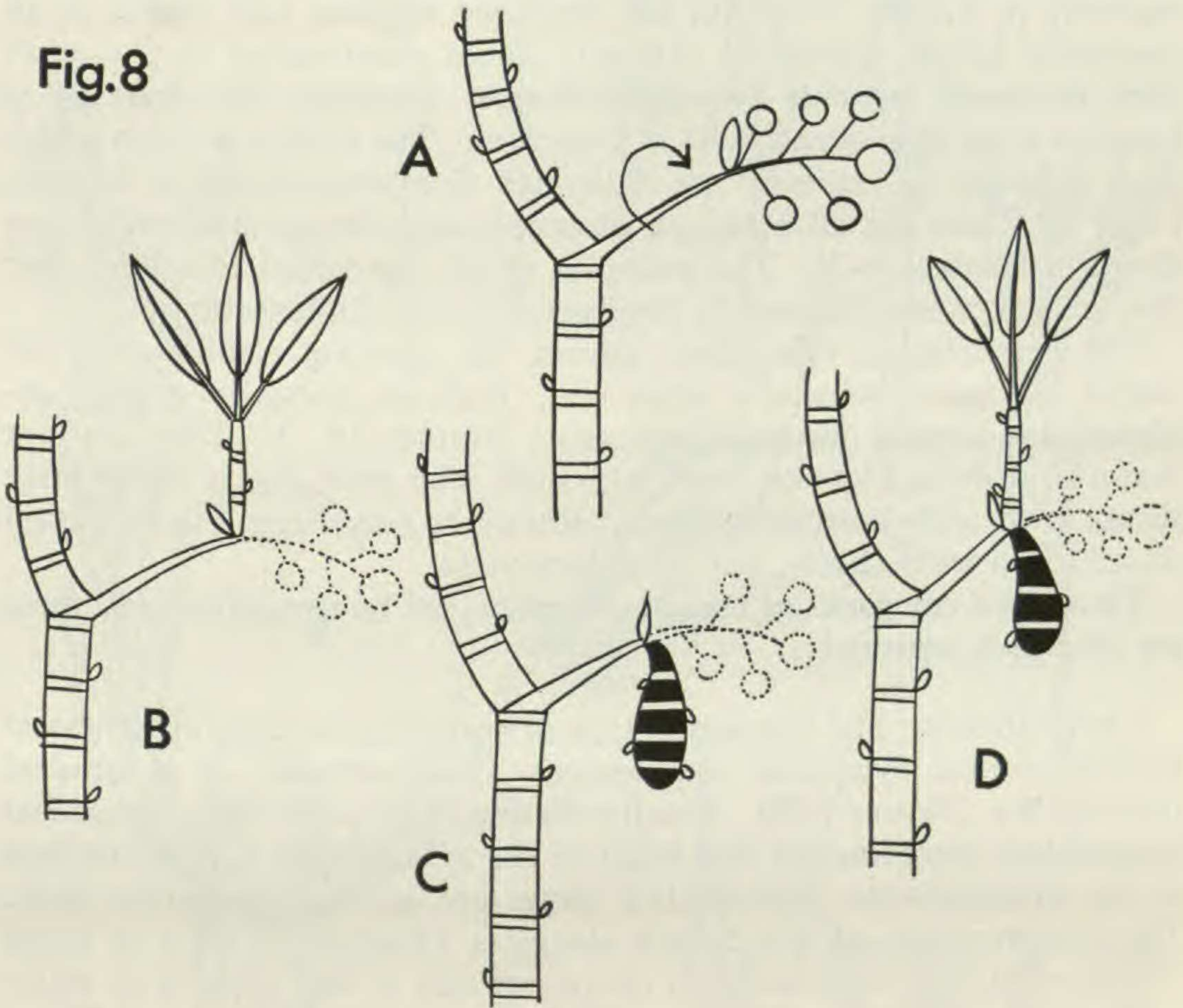
Fig. 7

FIGURES 7 and 8. **Cordyline terminalis,** shoot morphology represented diagrammatically. Leafy shoots are represented in outline with each node (double line) bearing a bud. Rhizomes shown solid black with each node (white line) bearing

Fig.8

a bud. Inflorescence represented by branched structures with circles; sites of former inflorescences are represented by dotted outline.

FIGURES 7 A–K. Branching on vegetative parts. A, sapling axis with original seedling axis displaced (arrow); B, forking of sympodium by production of two axillary branches below a terminal inflorescence; C, forking of stem by production of two axillary branches below injured or decapitated apex; D, leafy shoots from upper side of a leaning stem; E, leafy shoot from basal buds of an erect stem; F, aërial rhizome turning erect as a leafy shoot, the original rhizome producing a branch rhizome; G, leafy reversion shoot, flowering; branch rhizome itself branched; H, leafy shoot arising directly from rhizome at base of an erect sympodium; I, rhizome on lower side of leaning branch, branching *proximally* behind intact apex; J, rhizome on lower side of a leaning branch, branching *distally* behind injured or decapitated apex; K, typical position of aërial rhizomes on leafy shoots, on lower surface of a leaning branch, and at base of an erect shoot. Specimens which illustrate some of these diagrams are: A = FIGURE 6; B = FIGURE 14; C = FIGURE 9; F = FIGURES 18–20 (various ages).

FIGURES 8A–D. Vegetative proliferation at base of inflorescence. A, terminal inflorescence evicted by an axillary branch, the lowest bract subtending a flower-bearing branch (the twist of the base of the inflorescence is shown by the arrow); B, the same, with the lowest flowering branch replaced by a leafy shoot; C, the same, with the lowest flowering branch replaced by an aërial rhizome; D, the same, with the lowest flowering branch replaced by a leafy shoot plus a rhizome. Specimens which illustrate these diagrams are: A = FIGURE 11; B = FIGURES 21, 22; C = FIGURE 23.

with the descending scale-bearing rhizome. This is represented diagrammatically in FIGURE 7 A, with the displaced seedling axis shown as an apparently lateral appendage (arrow). Shoot construction in the adult plant eventually becomes seemingly diverse. However, this diversity is based on a few very simple rules of branching. The various ways in which these rules can be expressed are illustrated diagrammatically in FIGURES 7 and 8. These are all based on observed examples some of which are shown in FIGURES 9–26. The examples which correspond to a particular diagram are cross-referenced in the legends to these illustrations.

The morphological rules which govern this apparent elaborateness are simple. All leaves subtend a single bud. Buds are normally strongly inhibited and remain inconspicuous (e.g., FIGURE 14; b. They are not drawn to scale in FIGURES 7 and 8). Buds may grow out as either leafy shoots or as scale-bearing rhizomes. Rhizomes may become transformed directly into leafy shoots, but never vice-versa.

Three main categories of branch expression can be recognized, and these are described separately.

Leafy shoots. The commonest type of branching in undisturbed shoots involves normal sympodial development by substitution of a terminal inflorescence (FIGURE 7 H). Usually the bud in the axil of the foliage leaf immediately preceding the first bract of the inflorescence (i.e. at the base of the long peduncle (FIGURE 13), grows out as the substitution shoot. The first internode of this branch elongates (FIGURE 11, int.) to about the same extent as internodes on the parent axis so that there is no major articulation in the axis of the sympodium at the level of branching. Where buds from two successive nodes grow out, the sympodium itself branches and the axis is forked (FIGURES 7 B; 14). In this type of substitution growth, in which there is little delay in the development of the bud, its prophyll usually has a distinct lamina (FIGURE 12, prophyll) and the transition to foliage leaves along the branch is abrupt. Thus the second or third leaf of the continuing shoot has a more or less normal shape and size (FIGURE 12).

Essentially the same development occurs in the outgrowth of one or more buds below a damaged or decapitated apex as shown in FIGURES 7 C and 9. However, in these examples the bud has previously been subjected to a long period of inhibition. This is reflected in the outgrown shoot which has a short, scale-like prophyll without any indication of a lamina (FIGURE 10, prophyll) together with a longer series of transitional leaves before the normal foliage leaves are developed (FIGURE 10). Another difference is that the first few internodes do not elongate and there is consequently a more pronounced articulation at the insertion of the branch.[1]

Axillary buds on the upper side of leaning branches may grow out as leafy shoots (FIGURE 7 D). Buds at the base of tall erect stems may also

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[1] These differences between early ("precocious") and late-developing branches correspond to those seen in woody dicotyledons, where they have been distinguished as "sylleptic" and "proleptic" shoots (Tomlinson & Gill, unpublished).
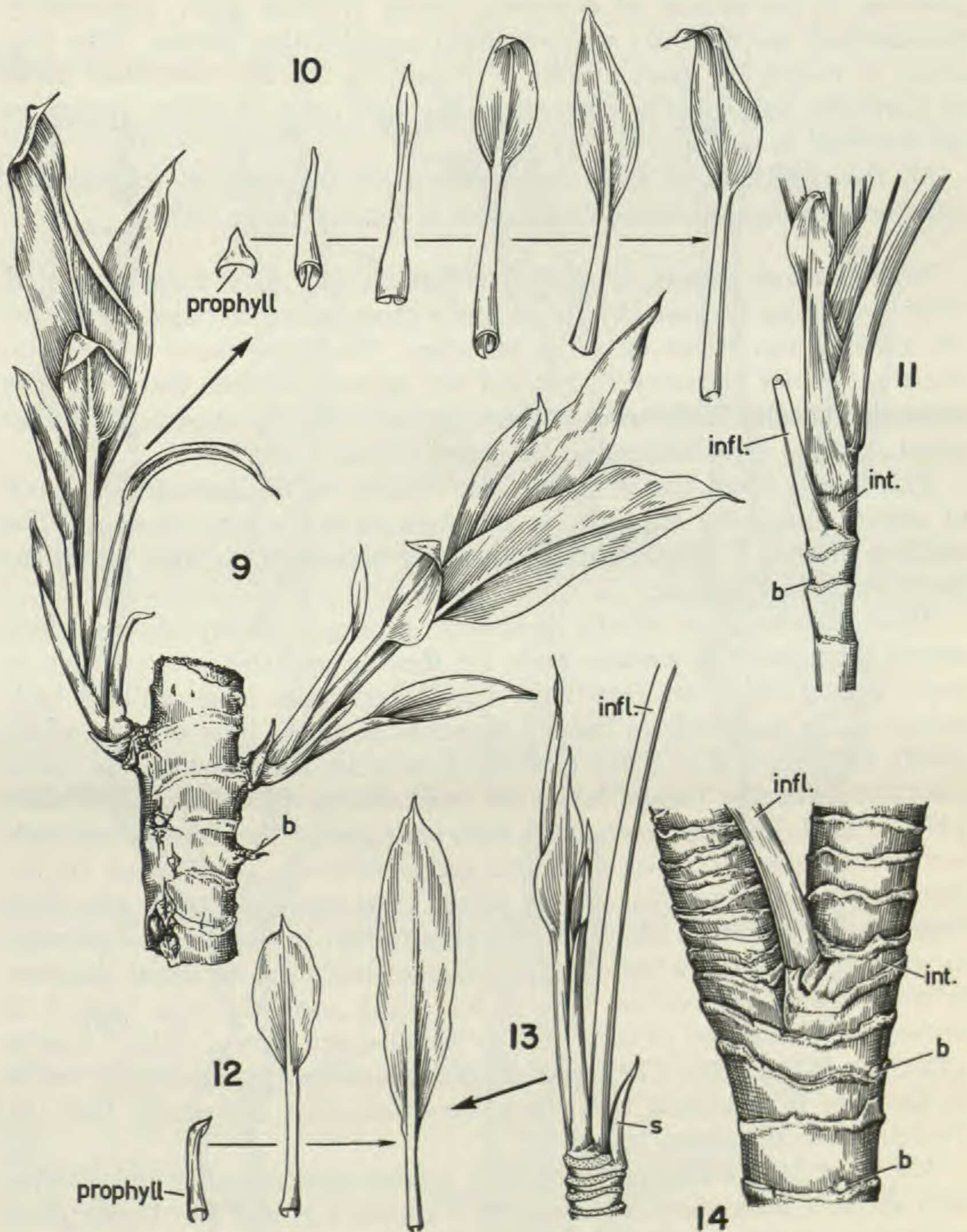
FIGURES 9–14. **Cordyline terminalis**, outgrowth of buds as leafy shoots. 9, two renewal branches below a decapitated apex, $\times$ 1/2; 10, six successive leaves from base of one of the branches shown in FIGURE 9, $\times$ 1/2, prophyll (first leaf) to left; 11, renewal shoot below terminal inflorescence only base of which (infl.) is shown, $\times$ 1/2, int. = first internode on renewal shoot; 12, three successive leaves from base of the branch shown in FIGURE 11, $\times$ 1/6, prophyll (first leaf) to left; 13, development of shoots from two buds below a terminal inflorescence, $\times$ 1/2, the right-hand (lower) shoot (S) at a much earlier stage than the left-hand (upper) shoot; 14, forking sympodium $\times$ 1, produced by equal development of two buds below a terminal inflorescence (infl.); int. = lowest internode of right-hand branch; b = inhibited buds. Diagrams which correspond to these illustrations are: 9 = FIGURE 7 C; 14 = FIGURE 7 B.

grow out in the manner of epicormic shoots (FIGURE 7 E), presumably because they are distantly removed from an inhibiting source. This tendency to branch by basal suckers is responsible for the "shrubby" habit of *Cordyline terminalis* in contrast to the tree habit of other species, as we described in our introductory paper.

All these methods of shoot development are precisely as reported for other arborescent Agavaceae (Tomlinson & Zimmermann, 1969).

Rhizomatous shoots. *Cordyline terminalis* does differ from almost all other Agavaceae because the rhizomatous shoot which is characteristic of the seedling also occurs on aërial branches. For convenience we refer to these as "aërial rhizomes," although we appreciate that there may be semantic difficulty in referring to above-ground shoots as rhizomes. Similar aërial rhizomes are developed in *Cordyline stricta*.

This type of shoot can, of course, also develop on the underground parts of mature plants, for example, as a branch of an existing rhizome. The seedling rhizome is therefore distinctive only because it occupies a particular place in the life cycle.

Aërial rhizomes are strictly positively geotropic, fleshy shoots which always originate from axillary buds, i.e. they occupy the same position as leafy shoots. However, they most usually originate from axillary buds either on the *lower* side of leaning branches or at the base of erect aërial shoots (FIGURE 7 K). They typically bear scale leaves which are spirodistichous, like the foliage leaves on erect shoots (Tomlinson & Fisher, 1971, p. 467). Like the erect shoots each scale leaf of the rhizome subtends a single axillary bud which is also strongly inhibited (e.g. FIGURE 16, b). Numerous root primordia are produced (FIGURES 16–19, r) but these remain as short initials which only develop further in a moist environment, as when the rhizome is buried. The range of leaf form on aërial rhizomes is considerable and varies from scales which are otherwise typical of underground rhizomes (FIGURE 15) to leaves which have a distinct lamina (FIGURES 16 and 17). The larger of these resemble the transitional leaves at the base of a branch which has developed from a dormant bud (cf. FIGURE 10 and FIGURES 16 and 17).

The apex of the rhizome itself may indeed turn upwards and develop into an erect leafy shoot, as shown in FIGURES 7 F and 18. Under these circumstances a new aërial rhizome usually develops from an axillary bud, either on the original rhizome (FIGURE 7 F) or on the leafy shoot into which the rhizome has been transformed (FIGURE 7 G). Specific examples of this are shown in FIGURE 19 (early stage) and FIGURE 20 (late stage). The leafy shoot into which the rhizome has become transformed may grow on to produce a typical flowering sympodium (FIGURE 7 G).

Underground rhizomes can also give rise directly to leafy shoots. This occurs when the axillary (or even apical) bud of an underground rhizome grows directly into a leafy shoot (FIGURE 7 H).

Aërial rhizomes may also "mimic" the pattern of branching of leafy shoots. Injured or decapitated aërial rhizomes may be substituted by new
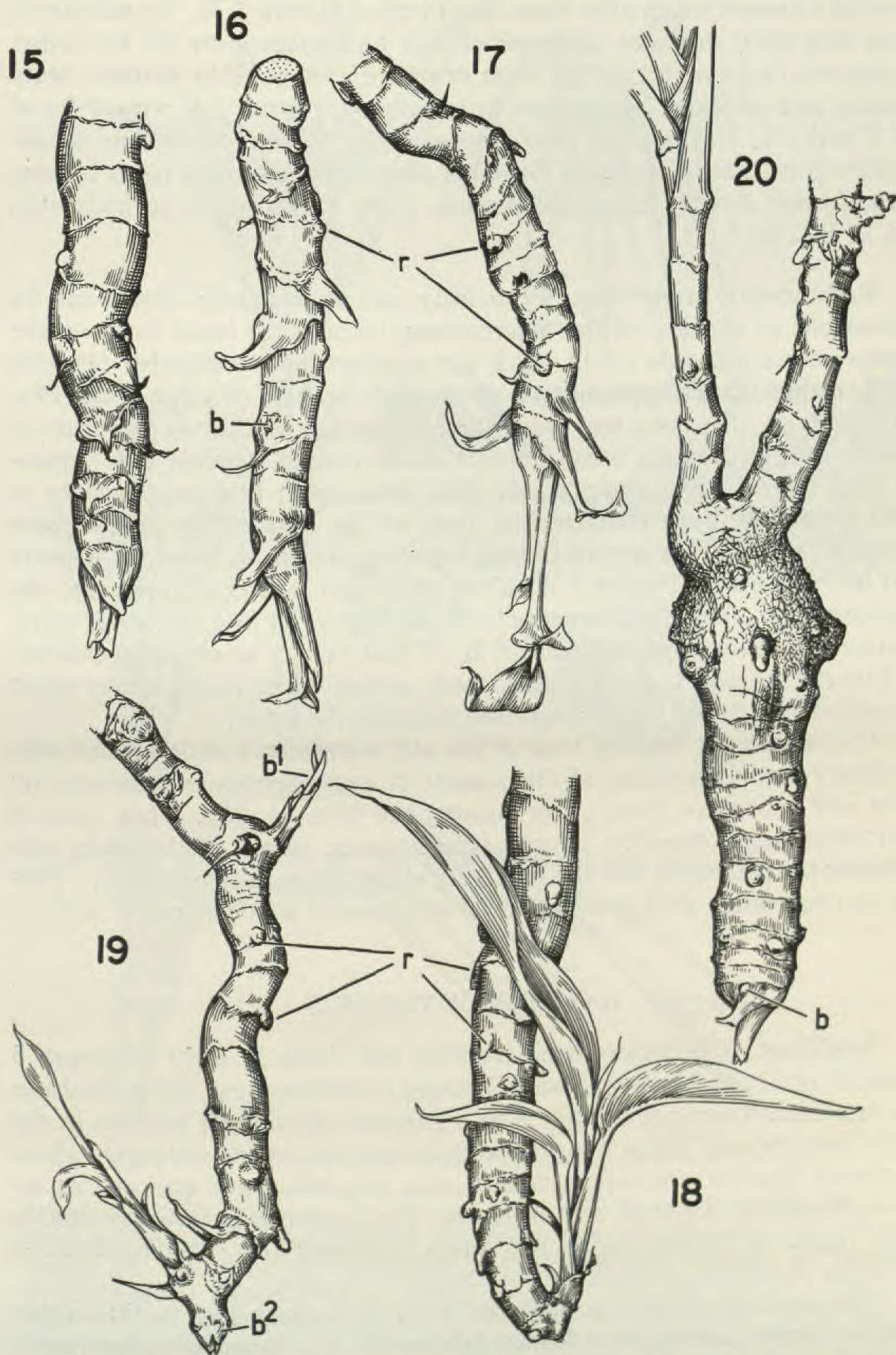
FIGURES 15–20. Cordyline terminalis, aërial rhizomes, all × 1. 15, typical aërial rhizome with scale leaves; 16 and 17, the same, but with distal leaves developing incipient (FIGURE 16) or quite pronounced (FIGURE 17) blades; 18, aërial rhizome with distal end turning erect as a leafy shoot; 19, similar, but with a basal bud (b¹) initiating a leafy shoot, and a distal bud (b²) ini-

lateral rhizomes which arise from distal buds (FIGURE 7 J). In uninjured, but long aërial rhizomes, proximal axillary buds often grow out as further rhizomes (FIGURE 7 I). The "mirror-image" relationship between leafy shoots and rhizomes is suggested in comparing FIGURE 7 C with 7 J and 7 E with 7 I. Unlike aërial shoots, however, in rhizomes there is no substitution growth associated with flowering since aërial rhizomes never become transformed directly into inflorescences (they may become so indirectly, as in FIGURE 7 G).

Peduncular branching. Both leafy and rhizomatous shoots can be developed at the base of the inflorescence, because the basal bract on the inflorescence subtends a bud which can grow out as a vegetative (FIGURE 25), rather than a reproductive (flowering) branch (FIGURE 24). Proliferation at this node may be complex, because of the development of buds subtended by the basal prophyll of the branch, whether it is vegetative or reproductive (FIGURE 26). This lower bract is always brought to the upper side by a characteristic twist of the base of the inflorescence axis. In this way the spirodistichous leaf arrangement of the shoot appears to be interrupted (FIGURE 8 A) although in fact it is continuous into the inflorescence. This "inflorescence" bud may grow out in a variety of ways, either as a leafy shoot (FIGURES 8 B, 21 and 22), or as an aërial rhizome (FIGURES 8 C; 23). Both a leafy shoot and an aërial rhizome may occur together (FIGURE 8 D) although one precedes the other.

It is significant that the base of the old inflorescence stalk retains only primary tissue, regardless of the amount of secondary tissue developed by the new vegetative shoot at its lowest node (FIGURE 23). Thus there is no secondary connection between the vascular tissue of the main axis (below the peduncle) and the new leafy shoot (above the peduncle). This is an observation with considerable developmental significance.

ANATOMY OF THE AXIS

Seedling. The underground seedling axis, both at early (FIGURES 3 and 4) and late (FIGURES 5 and 6) stages of development, never produces a cambium. There are usually 3 to 4 primary amphivasal bundles in the first internode and up to 8 to 9 bundles in the internode at soil level. These primary bundles are arranged in a ring and often are enclosed in an endodermis-like layer of sclerenchyma. The cambium is initiated first in the region of the axis at, or just above, soil level (as at internode X in FIGURE 4), and is active distally throughout the axis.

The seedling rhizome is produced from an axillary bud in this region where cambial activity is initiated (FIGURE 5, b). Vascular connection is

tiating a new aërial rhizome; 20, older stage with massive aërial branch rhizome (below) developed where a parent rhizome (upper left) has turned erect as a leafy shoot (upper right); b = dormant or developing buds; r = root primordia. A diagram corresponding to FIGURES 18–20 is given in FIGURE 7 F.
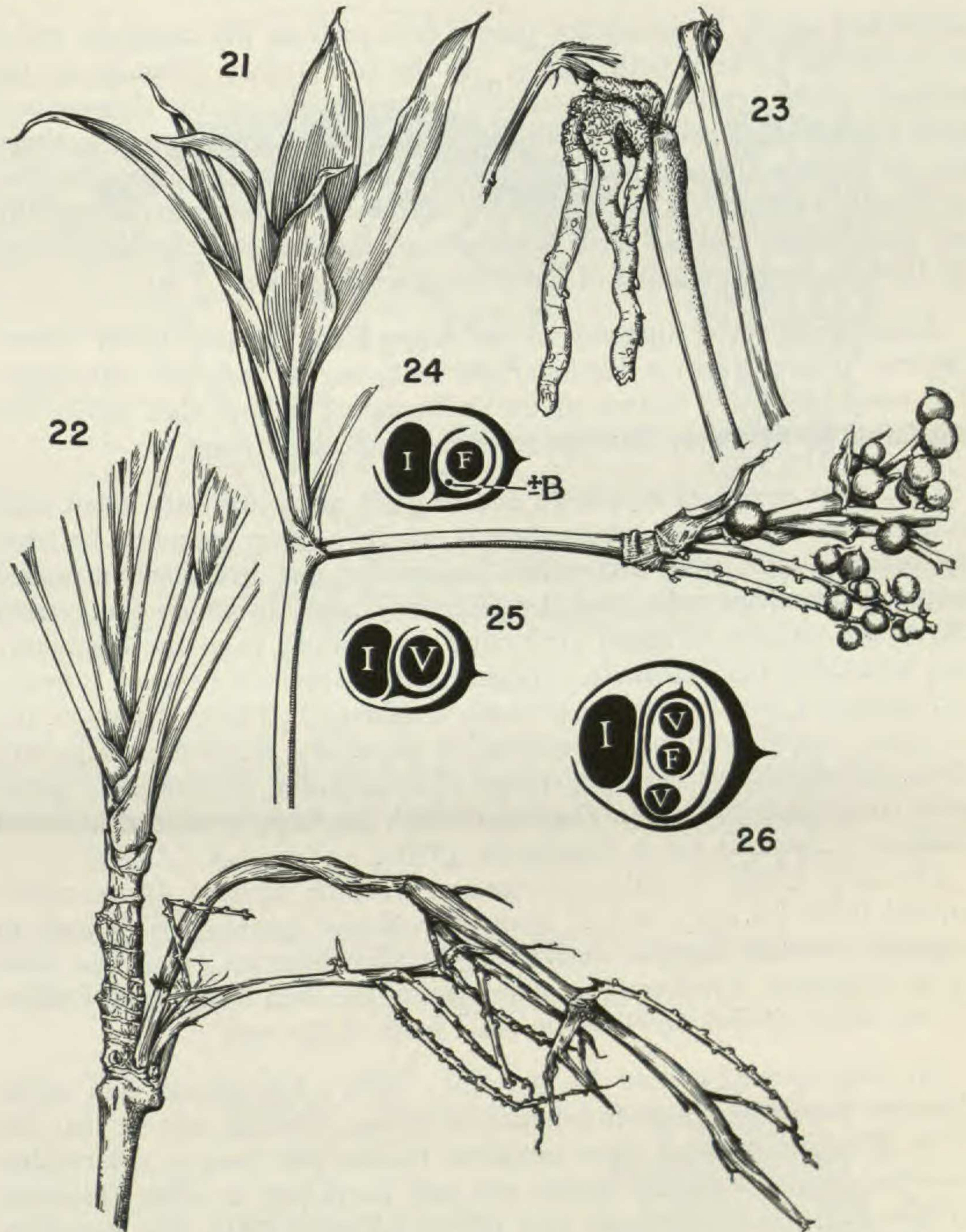
FIGURES 21–26. **Cordyline terminalis**, proliferating inflorescences, all × 1. 21, vegetative branch developing as a leafy shoot, the simple example shown diagrammatically in FIGURE 25; 22, older stage of leafy shoot with abundant secondary tissue, the inflorescence axis below this still retaining only primary tissue; 23, vegetative branch developing as a branching rhizome; 24, diagram of first node of inflorescence, I = main axis; F = flowering branch; a bud (B) may or may not be subtended by the first leaf on the branch (prophyll) as shown; 25, diagram of first node of inflorescence, proliferating vegetatively by replacement of flowering branch by vegetative branch (V), either a leafy shoot or a rhizome; 26, diagram showing development of a flowering branch (F) and two vegetative branches (V) at the first node of a proliferating inflorescence, the two latter from buds both subtended by the prophyll; this probably accounts for the proliferation of several branches in FIGURES 22 and 23, all seemingly from the same node. Habit diagrams corresponding to these specimens are: 21, 22 = FIGURE 8 B; 23 = FIGURE 8 C.

established mainly by secondary tissues derived from the cambium which is continuous between both organs. At the soil surface (FIGURE 6) the anatomy of the axis is often intermediate between that of the rhizome and stem (as described below). If the junction of rhizome and stem is above the soil surface, the proximal region of the rhizome is stem-like. In older seedlings the junction of leafy shoot and rhizome is neither morphologically nor anatomically obvious since the tissue of the axis is secondary except for the few primary bundles of the original seedling axis.

Adult axes. The anatomy of the three kinds of axis (leafy shoot; rhizome; inflorescence) is dissimilar and each may be described separately. The most distinctive feature of the inflorescence axis is that unlike the vegetative axes it never develops secondary vascular tissues.

(a) LEAFY SHOOT (FIGURES 27 and 28). In a mature leafy shoot with well-developed secondary tissues there is usually a sharp boundary between the primary zone, with thin-walled, unlignified and irregularly-arranged ground parenchyma cells, and the secondary zone, in which the ground tissues are radially arranged (reflecting their origin from the cambium) and with thick, lignified walls. There is little distinction between primary and secondary bundles because both are amphivasal. The sharpness of the boundary depends also on the amount of secondary establishment growth which the shoot may have undergone. The situation in *Cordyline* seems quite comparable to that in *Dracaena* which has been described in detail elsewhere (Zimmermann & Tomlinson, 1970).

The outer cortex is chlorenchymatous and the amount of secondary cortical tissue (if any) derived from the vascular cambium is difficult to establish, because cambial derivatives in this direction soon lose their radial alignment. Periderm (not developed in the stem from which FIGURE 27 was taken) is well developed in older parts of the axis.

(b) RHIZOME (FIGURES 29 and 30). Both underground and aërial rhizomes are similar in their internal structure, differing only in that the aërial rhizomes produce more periderm tissues and have a chlorenchymatous cortex. Secondary tissues are well developed in older rhizomes, but the vascular bundles are very diffuse (FIGURE 29). The boundary between primary and secondary tissue is indistinct because ground parenchyma in both regions remains unlignified. The secondary tissue, however, shows clear radial seriation of this parenchyma. Vascular bundles are again amphivasal, the secondary bundles being narrower than corresponding bundles in the leafy shoots (cf. FIGURES 28 and 30). The vascular cambium can be recognized much closer to the shoot apex in the rhizome compared with the leafy shoot, and this probably accounts for some of the differences between the two types of organ.

(c) INFLORESCENCE AXIS. This is strikingly different from the axis of the leafy shoot, of which it is a morphological extension, in that a vascular cambium is never developed (FIGURE 31). Most of the vascular bundles are collateral (FIGURE 32); they are narrower and more compact
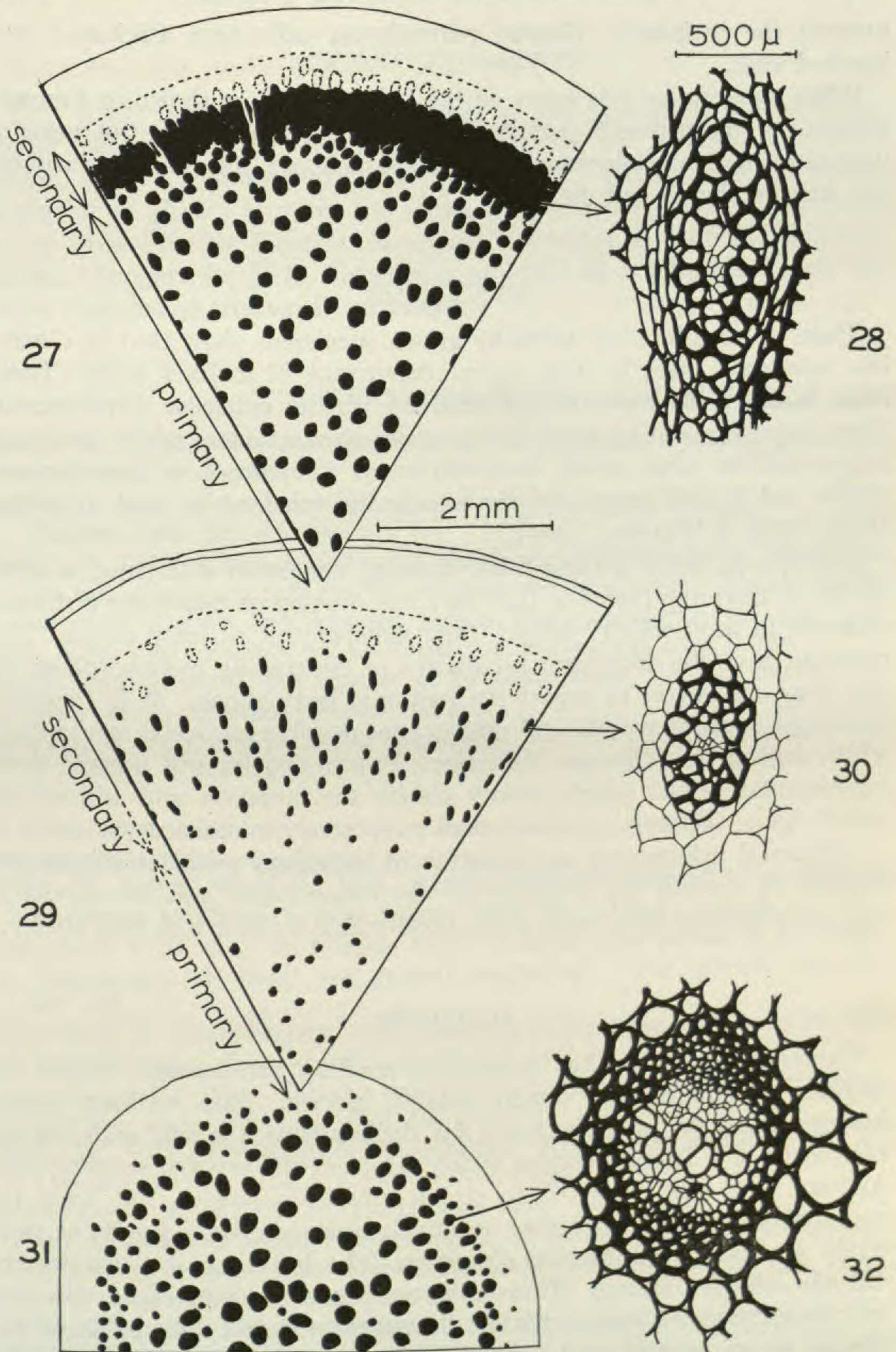
FIGURES 27–32. *Cordyline terminalis*, camera lucida drawings illustrating anatomy of different kinds of axes in transverse section. 27, mature leafy shoot, boundary between primary and secondary tissue quite distinct; 28, detail of an amphivasal secondary vascular bundle; 29, mature aërial rhizome, boundary between primary and secondary tissue indistinct; 30, detail of an amphivasal secondary vascular bundle; 31, mature inflorescence axis, no secondary vascular tissue; 32, detail of a collateral primary vascular bundle.

towards the periphery. Ground parenchyma cells have thickened and lignified walls.

When a vegetative axis arises on the inflorescence, as shown in FIGURES 22 and 23, the peduncle persists and produces a periderm, but never a vascular cambium. Inflorescences of comparable age, but without a vegetative branch, shrivel and die.

DISCUSSION

These observations on naturally grown specimens show that in *Cordyline terminalis* there is strict apical dominance of axillary buds. These buds, however, do have the potential for further extensive development. They may grow out as leafy shoots under circumstances which are quite comparable for other woody monocotyledons (Tomlinson & Zimmermann, 1969) and indeed seemingly for woody dicotyledons as well (Phillips, 1969; Smith & Wareing, 1964).

A unique property of these buds, however, compared with those in other genera of flowering plants is that they can develop as positively geotropic rhizomes in ways which "mimic" their development as leafy shoots. The rhizomes have the additional peculiarity of undergoing metamorphosis so that they can revert to negatively geotropic leafy shoots. It is therefore of interest to seek experimental evidence for possible hormonal mechanisms which control this divergent behavior. Future articles will present these experimental results which greatly clarify the situation and add to our knowledge of factors controlling shoot morphology in monocotyledons.

Additional information on initiation of secondary vascular tissues will attempt to explain the inability of the inflorescence axis to develop a vascular cambium even when it has proliferated a shoot with this ability.

SUMMARY

Cordyline terminalis has hypogeous seedling germination, unlike the epigeous germination of closely related species. Late seedling stages, however, show features diagnostic for the genus as a whole, with the development of a lateral rhizome which displaces the original seedling axis. Axillary buds are subjected to strong apical dominance, but have the potential to grow out as either negatively geotropic leafy shoots or positively geotropic, scale-bearing rhizomes. The latter can be transformed directly into the former. These different kinds of shoot expression seen on naturally grown individuals are described in detail. The value of this species as an experimental subject is emphasized. In outlining the distribution of secondary tissues in the various parts of the plant, the inability of the inflorescence axis to develop a vascular cambium is pointed out, a peculiarity which is particularly striking in parts which are below a vegetative proliferation. These observations provide a background for future experimental work.

ACKNOWLEDGMENTS

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